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Morphological variation in *Pteropus lombocensis* (Chiroptera: Pteropodidae) in Nusa Tenggara, Indonesia

D.J. Kitchener[1], W.C. Packer[1] and Maharadatunkamsi[2]

[1]Western Australian Museum, Francis Street, Perth, Western Australia 6000
[2]Museum Zoologicum Bogoriense, LIPI, Jalan Ir. H. Juanda 9, Bogor, Indonesia 16122

Abstract – Recent terrestrial vertebrate faunal surveys in Nusa Tenggara, Indonesia, collected specimens of *Pteropus lombocensis* from islands from which the species had not previously been reported (Sumbawa, Lembata and Pantar), as well as from Lombok, Flores and Alor Islands.

A univariate and multivariate statistical analysis of 28 morphological (skull dentary, dental and external) characters showed that adult *P. lombocensis* was not sexually dimorphic, but that significant variation occurred, particularly in dental characters, between the island populations.

Two subspecies are recognised in *P. lombocensis*. These are the western form, *P. l. lombocensis* Dobson, 1878 (Lombok and Sumbawa Islands), and the eastern form, *P. l. heudei* Matschie, 1899 (Flores, Lembata, Pantar and Alor).

INTRODUCTION

Andersen (1912) stated that the members of the *Pteropus lombocensis* group were characterised by their small size (forearm length 94–127 mm); short and broad rostrum; conspicuously reduced M_3, M^2 and I_1; I_1, one-quarter to one-sixth the bulk of I_2; ears moderate or short; tibia furred dorsally, except in the species from the Caroline Islands; hair pale or dark brown dorsally with a buffy mantle, except in the Caroline Islands species which is a darker brown.

Andersen (1912) recognised two species from the *P. lombocensis* group in Indonesia; these were both restricted to Nusa Tenggara. They were *P. lombocensis* Dobson, 1978 (Lombok Island – the type locality and Flores Island) and *P. solitarius* K. Andersen, 1908 (Alor Island). The form *P. heudei* Matschie, 1899 from Flores Island, was originally described by Heude (1896) as *P. tricolor* but this name was preoccupied. Andersen (1912) and Hill in Corbet and Hill (1992) considered *P. heudei* synonymous with *P. lombocensis*. Hill (*op cit.*) also considered *P. solitarius* a subspecies of *P. lombocensis*.

A series of terrestrial vertebrate surveys throughout islands in southern Indonesia between 1987 and 1993 by staff from both the Western Australian Museum and Museum Zoologicum Bogoriense, resulted in the collection of a series of *P. lombocensis* from Lombok, Sumbawa, Flores, Lembata, Pantar and Alor islands. This is a much more extensive series of specimens than was hitherto available for study. They are also the first records of the species from Sumbawa, Lembata and Pantar islands.

This paper reports on an examination of morphological variation among island populations of *P. lombocensis* and evaluates this variation in the context of their subspecific taxonomy.

MATERIALS AND METHODS

A total of 30 adult specimens (listed in specimens examined section) was examined. These were from Lombok Island (8♂♂, 3♀♀); Flores Island (1♂, 1♀); Lembata Island (2♂♂, 6♀♀); Pantar Island (4♀♀) and Alor Island (2♂♂, 3♀♀). Additionally four subadult specimens were examined from Sumbawa Island. The localities of these specimens are shown in Figure 1. All specimens are currently lodged in the Western Australian Museum.

Eighteen measurements of skull, dentary and dental characters and 10 of external body characters (all in mm) were recorded from adult specimens.

The measurements recorded were GSL, greatest skull length; CBL, condylobasal length; PL, palatal length; MFW, mesopterygoid fossa breadth; RL, rostrum length, from anteriormost internal margin of orbit to posterior margin of nares; IOB, minimum interorbital breadth; ZW, zygomatic width; BB, braincase breadth above zygoma; DL, dentary length; C^1C^1, width across C^1 to C^1 from the labial side at alveoli; P^4P^4, palatal breadth measured between posterior upper premolars; M^1M^1, width across M^1 to M^1 from the labial side at alveoli; C^1M^2, upper maxillary tooth row length; C_1M_3, lower canine to M_3 length; P^3L, middle upper premolar crown length; P^3B; middle upper premolar crown breadth; M^1L, first upper premolar

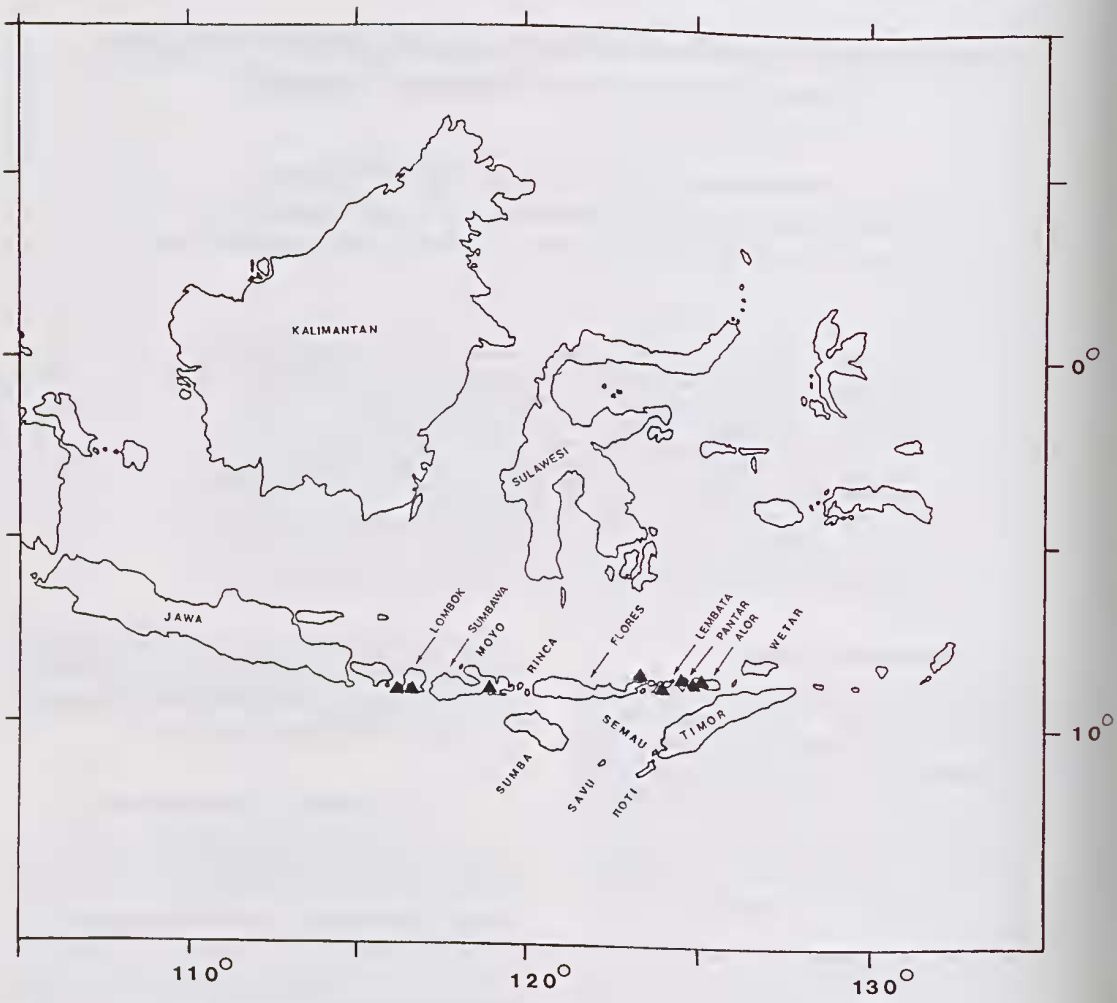

Figure 1 Locality of *Pteropus lombocensis* used in this study.

Table 1 Measurements, in mm, for skull, dentary, dental and external body characters (see Materials and Methods section for explanation of character codes) of adult *Pteropus lombocensis lombocensis* (Lombok Island) and *P. lombocensis heudei* (Flores, Lembata, Pantar and Alor Islands). N, sample size; $\bar{X}$, mean; SD, standard deviation, MIN, minimum; and MAX, maximum.

		GSL	CBL	PL	MFW	RL	IOB	ZW	BB	DL	C^1C^1	P^4P^4	M^1M^1	C^1M^2
P. l. lombocensis	N	11	11	11	11	11	11	11	11	11	11	11	11	11
Lombok I.	$\bar{X}$	55.03	53.11	29.73	6.98	14.58	8.08	30.24	21.12	41.91	10.63	9.54	15.61	20.06
	SD	0.99	0.89	0.73	0.23	0.51	0.38	0.59	0.49	0.75	0.33	0.36	0.67	0.40
	MIN	53.18	51.23	28.22	6.60	13.72	7.36	29.43	20.30	40.28	10.13	8.82	14.26	19.16
	MAX	56.98	54.22	31.06	7.29	15.38	8.79	31.02	21.82	43.09	11.07	10.01	16.89	20.58
P. l. heudei	N	18	18	18	18	18	18	18	18	18	18	18	18	18
Flores-Lembata	$\bar{X}$	54.09	52.03	29.14	7.09	14.30	7.87	29.79	20.91	40.62	10.40	9.51	15.05	19.28
-Pantar-Alor	SD	1.05	1.15	0.70	0.35	0.57	0.22	0.72	0.43	0.85	0.31	0.34	0.30	0.32
	MIN	52.35	50.06	27.97	6.65	13.34	7.47	28.21	19.97	38.93	9.89	8.91	14.45	18.82
	MAX	55.83	53.69	30.36	7.88	15.25	8.33	30.90	21.65	41.85	10.95	10.20	15.57	19.88

crown length; M^1B, first upper premolar crown breadth; FA, forearm length; D2M, digit 2 metacarpal length; D3M, digit 3 metacarpal length; D3P1, digit 3 phalanx 1 length; D3P2, digit 3 phalanx 2 length; D4M, digit 4 metacarpal length; D5M, digit 5 metacarpal length; TIB, tibia length; PES, pes length; EAR, ear length.

The skull, dentary and dental characters were measured to 0.01 an accuracy of mm, while the external characters were measured to 0.1 mm. Pelage descriptions follow the colour terminology of Smithe (1975).

Adults were diagnosed as those specimens with the following sutures fused: basioccipital-basisphenoid, basisphenoid-presphenoid and palatine-maxillary.

The effect of sex and island on all characters was examined by standard multiple regressions (where all effects were assessed simultaneously) for those islands for which we had specimens of both sex. Pantar Island was excluded because we had only female specimens from that island.

Stepwise canonical variate (discriminant function) analyses (DFA) were run for skull, dentary, dental and external body characters using all characters measured, except for tibia length [because it had a significant interaction ($P<0.01$) between island and sex], for males and females combined.

STATISTICS: RESULTS AND DISCUSSION

Univariate statistics

Mean, standard deviation, minimum and maximum values and sample size for each island are presented in Table 1 for all characters measured.

Multiple regressions

Multiple regressions were run for skull, dentary and external characters on four islands (Lombok, Flores, Lembata and Alor). The results of this analysis are presented in Table 2. Because of the number of interactions being tested some of these tests may be significant by chance alone at $0.05 > P > 0.01$. Consequently, significance levels for this analysis were set at $P<0.01$.

Sex

No characters were significantly influenced by sex alone, but there was a significant ($F_{3,17} = 6.046$; $P = 0.005$) interaction between sex and island for tibia length. This interaction resulted from the tibia length for the male being much longer than the female (56.3 *v.* 50.4) on Flores Island, whereas on the other islands they were subequal in length.

Island

Some dental measurements only were significantly influenced by island alone. These were: C^1M^2 length ($F_{3,17} = 10.79$, $P<.001$); C_1M_3 length ($F_{3,17} = 44.52$, $P<.001$); P^3 breadth ($F_{3,17} = 8.94$, $P = 0.001$); and M^1 breadth ($F_{3,17} = 12.54$, $P = 0.001$).

Multivariate analysis

Because of the absence of any significant influence of sex, apart from the significant interaction between sex and island for tibia length, males and females were combined for all characters, except for tibia length, for the following DFA. Tibia length was excluded from this analysis.

The DFA was first run for the remaining 27 characters for all islands (Lombok, Flores, Lembata, Adonara, Pantar and Alor). This analysis extracted two significant functions which explained 92% of the variance (Figure 2). A total of 86.2% of individuals was correctly classified to their appropriate island. Three clusters were apparent from Figure 2. These were Lombok Island, Alor Island and a third group comprising Lembata, Flores and Pantar Islands. The DFA run on these three above groups, using all 27 characters, again extracted two significant functions that explained 100% of the variance, with 96.5% of individuals correctly classified to their appropriate group. Only

Table 1 (continued)

C_1M_3	P^3L	P^3B	M^1L	M^1B	FA	D2M	D3M	D3P1	D3P2	D4M	D5M	TIB	PES	EAR
11	11	11	11	11	11	11	11	11	11	11	11	11	11	11
22.69	3.88	2.97	5.13	2.80	117.4	57.8	80.4	54.8	81.8	80.2	84.9	52.5	29.5	26.8
0.29	0.15	0.11	0.28	0.13	2.6	1.7	2.8	1.3	1.7	2.7	2.6	1.3	0.8	0.7
22.19	3.61	2.77	4.68	2.67	113.6	55.3	76.3	52.4	77.7	75.2	81.2	50.1	28.7	25.6
23.20	4.08	3.17	5.51	3.09	121.1	60.5	85.9	56.5	84.4	85.0	90.3	54.5	31.0	27.6
18	18	18	18	18	18	18	18	18	18	18	18	18	18	18
21.09	3.81	2.74	4.82	2.53	114.6	56.2	78.9	53.2	81.9	78.5	82.9	51.2	28.9	27.5
0.54	0.16	0.11	0.33	0.10	4.3	2.2	2.5	2.3	2.6	2.9	3.1	2.3	1.0	1.0
19.28	3.53	2.51	4.20	2.29	107.4	50.9	73.2	49.2	76.3	72.3	75.6	46.4	26.5	25.9
21.87	4.14	2.92	5.36	2.64	122.0	60.1	83.4	56.1	86.2	83.9	87.7	56.3	30.2	29.5

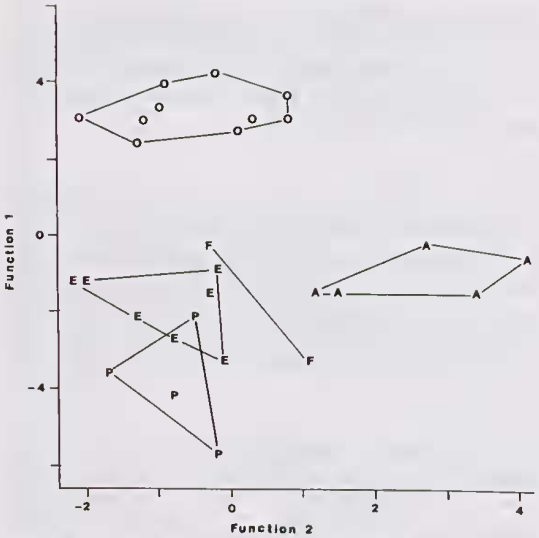

Figure 2 Plot of Functions 1 and 2 from canonical variate analysis of five island groups (Lombok, O; Flores, F; Lembata, E; Pantar, P; and Alor, A) based on 27 characters (see text), with males and females combined.

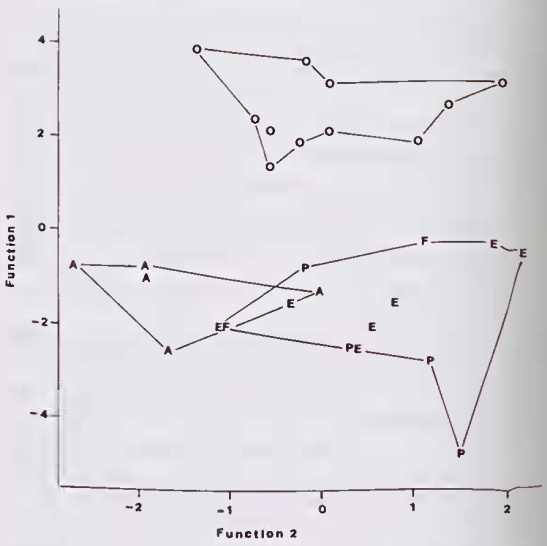

Figure 3 Plot of Functions 1 and 2 from canonical variate analysis of three island groups (Lombok, Alor and Flores-Lembata-Pantar) and a reduced set of 5 characters (see text), with males and females combined. Abbreviations for island populations as for Figure 2.

one Alor specimen was misclassified (to the Lembata-Flores-Pantar group). Because the number of characters in this latter analysis (N = 27) greatly exceeds the sample size of the smallest group (Alor, N = 5) the DFA was repeated for these three groups using a reduced set of five characters. This reduced set was selected from this latter analysis to minimise Wilk's lambda. These five characters were: C_1M_3 length, M^1 width, C^1M^2 length, rostrum length and digit 4 metacarpal length. The DFA using this reduced set of characters produced similar DFA plots to those based on the three island groups using the 27 characters. Consequently, only results based on these five characters are detailed below. This DFA extracted two significant functions that explained all the variance (Figure 3). Function 1, which explained 87.9% of the variance, separated the Lombok Island group from the other two groups. The character with the canonical discriminant function coefficient that loaded heavily (>0.5) on Function 1 was C_1M_3 length (Table 3). This suggested that this character was an important discriminant between the Lombok Island population and the other populations. Function 2, which explained 12.1% of the variance, partially separated the Alor Island population from the Flores-Lembata-Pantar population. The characters that loaded heavily (>0.5) on Function 2 were C^1M^2 length (1.02), rostrum length (0.94), digit 4 metacarpal length (0.73) and M^1 breadth (Table 3). This suggested that a number of dental, skull and external characters were involved in the partial separation of the Alor population from the other eastern Nusa Tenggara populations. A total of 89.7% of individuals was correctly classified to their appropriate island group. The Lombok Island population was most distinct, with 100% of its individuals correctly classified. All misclassifications occurred between the Alor population and those of the other eastern islands. One of the five Alor Island individuals was misclassified to the Flores-Lembata-Pantar group, while two of the 13 individuals in this latter group were misclassified to the Alor population.

Summary of multivariate analysis

The above analysis indicates that two broad morphological forms occurred among *Pteropus lombocensis* in Nusa Tenggara. These were the Lombok Island form (*Pteropus lombocensis lombocensis*) and a form involving the remaining eastern populations (Flores, Lembata, Pantar and Alor), in which the Alor population is slightly differentiated from the others. This differentiation of the Alor form from the other eastern populations is slight and is not considered to have taxonomic significance. Of the two named forms in these eastern Nusa Tenggara islands (*P. solitarius* – Alor and *P. heudei* – Flores), *P. heudei* has priority and becomes the subspecific name (*P. lombocensis heudei*) for this eastern form.

Table 2 Multiple regressions on sex and island populations (Lombok, Flores, Lembata and Alor) of *Pteropus lombocensis* for skull, dentary, dental and external body characters. F values are presented for the main effects and their interactions. For explanation of character codes see Material and Methods section. Significance levels are *, 0.05>P>0.01; **, 0.01>P>0.001; ***, P<0.001.

CHARACTER	MAIN EFFECTS SEX	MAIN EFFECTS ISLAND	INTERACTION SEX. ISLAND
GSL	1.319	1.455	0.079
CBL	0.750	2.082	0.064
PL	0.982	1.819	0.064
MFW	0.881	1.705	0.509
RL	0.290	0.466	0.339
IOB	2.596	0.870	0.533
ZW	0.176	0.697	1.967
BB	0.497	0.670	1.834
DL	1.582	3.028	0.581
C^1C^1	1.346	0.865	1.368
P^4P^4	0.002	1.589	1.924
M^1M^1	0.047	1.255	0.150
C^1M^2	0.044	10.788***	1.513
C_1M_3	4.902*	44.522***	2.232
P^3L	1.605	0.853	1.772
P^3B	2.178	8.942**	0.104
M^1L	0.108	1.382	0.926
M^1B	0.997	12.537***	0.677
FA	0.003	1.846	1.544
D2M	0.020	1.436	1.334
D3M	0.020	1.266	0.515
D3P1	0.504	2.116	1.288
D3P2	0.304	0.862	2.765
D4M	0.251	1.334	1.598
D5M	0.278	1.144	1.387
TIB	1.531	4.417*	6.046**
PES	3.685	1.877	2.023
EAR	0.098	2.446	0.626
Degrees of freedom	1,17	3,17	3,17

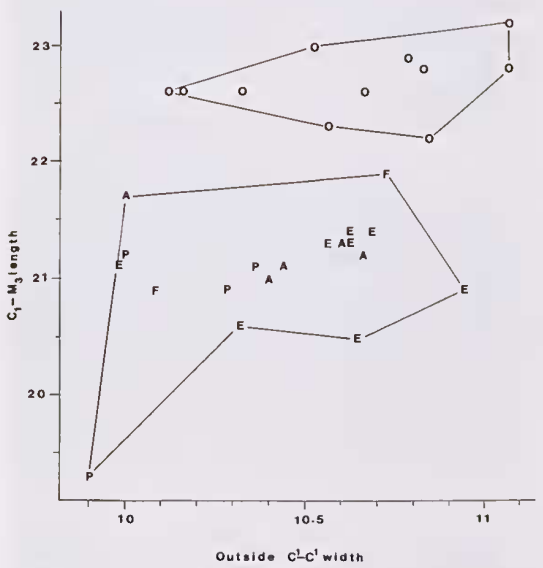

Figure 4 Plot of upper maxillary tooth row length *versus* width outside C^1C^1.

SYSTEMATICS

***Pteropus lombocensis lombocensis* Dobson, 1878**

Pteropus lombocensis Dobson, 1878: 34, pl. iii, fig. 2, pl. iv, fig. 4.

Holotype

Natural History Museum, London, Number 64.4.12.2, adult male, 'cabinet skin' and skull.

Type locality

Lombok Island, Nusa Tenggara.

Specimens examined

Lombok Island (all adults)

Desa Pelangan, 8°48'S, 115°56 E, 1♂, WAM M30603; Desa Kuta, 8°55'S, 116°15'E, 3♂♂ 1♀, WAM M30611–4; Matahari Inn, Near Kuta, 4♂♂ 2♀♀, WAM M(36108, 36155, 36158, 36172, 36174–5).

Sumbawa Island (all subadults)

Desa Daha, 8°45'S, 118°26'E, 3♂♂ 1♀, WAM M(31710–1, 31722, 31742).

Table 3 Canonical variate function coefficients from DFA between three groups of *P. lombocensis* (Lombok, Alor, and Flores-Lembata-Pantar) based on five characters (see text). Standardised values, followed by (in brackets) unstandardised values.

CHARACTER	FUNCTION 1	FUNCTION 2
C_1M_3	0.8254 (1.7860)	–0.1482 (–0.3207)
M^1B	0.4364 (4.0404)	–0.6423 (–5.9471)
C^1M^2	0.2916 (0.8321)	1.0210 (2.9131)
RL	–0.4357 (–0.7906)	–0.9400 (–1.7058)
D4M	–0.1074 (–0.0393)	0.7278 (0.2661)
CONSTANT	–51.1681	–30.9264
Variance explained (%)	87.9	12.1

Diagnosis

Averages larger than *Pteropus lombocensis heudei* for all characters except mesopterygoid fossa breadth, digit 3 phalanx 2 length and ear length (see Table 1). C_1M_3 is larger relative to width outside C^1C^1 (Figure 4). The colour of the collar at the neck, base of head, throat and upper chest is a darker Cinnamon – Cinnamon Rufous compared to Cream Color to Buff Yellow.

Description

See Andersen (1912: 266–9) for a detailed description of pelage, skull, dentary, teeth and palatal ridges.

Distribution

Lombok and Sumbawa Islands.

Remarks

The juvenile and subadult specimens from Sumbawa Island have pelage colour and teeth dimensions similar to the adult specimens from Lombok Island. They are referred to *P. l. lombocensis*.

***Pteropus lombocensis heudei* Matschie, 1899**

Pteropus heudei Matschie, 1899: 32.

Pteropus tricolor Heude, 1896: 177, footnote, pl. v. fig. 7 (teeth) (preoccupied).

Pteropus solitarius K. Andersen, 1908: 367.

Holotype

Andersen (1912: 269) states that "type presumably in the Zi-ka-wei Museum, near Shanghai".

Type locality

Flores Island, Nusa Tenggara.

Specimens examined

Flores Island (all adults)

Desa Ratulodong, 8°11'S, 122°52'E, 1♂ 1♀ , WAM M(32563, 32568).

Lembata Island

Desa Belang Watokob, 8°26'S, 123°22'E, 1♂ 5♀♀, WAM M(32152, 32154, 32178, 32211–2, 32455); Desa Boto, 8°31'S, 123°23'E, 1♂ 1♀, WAM M32453–4.

Pantar Island

Desa Batu Bakalang, 8°14'S, 124°18'E, 4 , WAM M37757–60.

Alor Island

Kota Kalabahi, 8°14'S, 124°32'E, 1♂ 3♀, WAM M37637–40; Desa Apui, 8°15'S, 124°43'E, 1♂, WAM M37996.

Diagnosis

Pteropus lombocensis heudei differs from *P. l. lombocensis* as described in the earlier diagnosis of that subspecies.

Description

See Andersen (1912: 269–71, Fig. 13) for a detailed description of pelage, skull, dentary and teeth (figured for *P. solitarius*) and palatal ridges.

Distribution

Flores, Lembata, Pantar and Alor Islands.

GENERAL DISCUSSION

Pteropus lombocensis is restricted to the volcanic islands of the inner Banda Arc, from Lombok Island in the west to Alor Island in the east. In this region it coexists with both the very large *Pteropus vampyrus* Linnaeus, 1758 (which occurs on Lombok Island and Sumbawa [Hill in Corbet and Hill 1992], Moyo, Flores and Kisar Islands [unpublished records]) and the large *Pteropus alecto alecto* Temminck, 1837 (which occurs on Lombok Island [Hill in Corbet and Hill 1992] and Rinca Island [unpublished records]).

In other parts of Nusa Tenggara, *P. lombocensis* is replaced by the similarly sized, and probably ecologically vicarious, *Pteropus griseus griseus* Geoffroy, 1810 and *Pteropus alecto morio* Andersen,

1908. *Pteropus g. griseus* occurs on Wetar Island (unpublished record), immediately to the east of Alor Island, and some other islands in the gondwanic outer Banda Arc (Timor and Semau Island [Goodwin 1979] and Roti Island [unpublished record]. A larger form of *P. alecto*, probably *P. alecto gouldi* Peters, 1867, also occurs on Timor Island [unpublished record]). *Pteropus alecto morio* occurs on Sumba and Savu Islands (Hill in Corbet and Hill 1992; unpublished records). *Pteropus vampyrus* occurs on two outer Banda Arc islands, Timor (Goodwin 1979) and Roti (unpublished report).

In conclusion, the small *Pteropus* species in Nusa Tenggara (*P. lombocensis*, *P. g. griseus*, *P. alecto morio*) show a pattern of distribution that is repeated by a number of other bat taxa. That is, a species that is widely distributed in the inner Banda Arc either differentiates morphologically into subspecies in the outer Banda Arc (Sumba, Savu, Roti, Semau, and Timor) or is replaced there by allied species (see Kitchener *et al.* 1994 a,b)

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